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A MIOCENE LEMUROID SKULL FROM EAST AFRICA

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A MIOCENE LEMUROID SKULL FROM EAST AFRICA

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In the early part of 1954 an examination of a small block of matrix from Rusinga Island, in the Kavirondo Gulf of Lake Victoria, revealed the greater part of a fossil lemuroid skull. The block was from the greyish beds of Shackleton's Kiahera Series (Shackleton, 1951). The anterior extremity of the skull, which fitted accurately the main specimen, was found *in situ* at site R.105*b* on Rusinga Island (for the general position of this site, reference should be made to the map in Le Gros Clark & Leakey, 1951). The field catalogue number of the skull is No. 1, 1954. The local deposits from which the specimen was obtained also yielded a number of fossil fruits and seeds. The skull is almost complete, but lacks the zygomatic arch, nasal bones and mandible. It is much larger than the fragmentary lemuroid skull previously described from site R.3 on Rusinga Island (Le Gros Clark & Thomas, 1952), and also shows marked differences in the morphological details of the cranial base. The morphological characters of the skull conform to the lorisiform, and not the lemuriform, type; in the following description, therefore, comparison is mainly limited to the Recent Lorisiformes.

Description of the Skull (Plate 1, figs. 1–4)

In its general size the fossil skull corresponds rather closely to the Recent genera *Perodicticus* and *Nycticebus*, but the brain-case is relatively less expanded and the palate conspicuously larger. The total length of the skull is 58 mm. and the maximum width of the brain-case 28·5 mm.

From the lateral aspect (Pl. 1, figs. 1, 2) the orbits appear unusually large, but this is partly illusory because the zygoma and the post-orbital bar are missing. The facial part of the skull is relatively abbreviated, as in *Perodicticus* and *Nycticebus*. The contour of the cranial roof forms a flattened arch and terminates posteriorly in a conspicuous nuchal crest similar to, but more pronounced than, that of *Galago crassicaudatus*. This is in marked contrast with the rounded occipital contour of other Recent Lorisiformes. The maxilla in its general shape and absolute dimensions is closely similar to that of *Perodicticus*. A single infraorbital foramen is present; herein it conforms with the usual arrangement in the Lorisiformes, except for *Perodicticus* in which the foramen is multiple in 60 per cent of specimens. No trace of a premaxillary suture can be detected. The nasal aperture, relatively larger than in any of the Recent Lorisiformes, has a maximum width of approximately 8 mm.; its lower border is separated from the palatal margin by about 1 mm. The supraorbital margin has been damaged by abrasion on both sides, and it is not possible to define its lateral extent precisely. On the left side it appears to meet the anterior

extremity of the temporal ridge at a sharp point, suggesting that it terminated in a supraorbital process but was not continued into a postorbital bar. However, the upper surface of the supraorbital process also shows a very small surface abrasion, and the possibility therefore remains that a slender postorbital bar may have been present in the intact skull.

Fine cracks on the medial wall of the orbit make it difficult to define the sutural pattern here completely, but a comparison of the two sides shows clearly that there is a relatively extensive orbital plate of the ethmoid of rectangular form, articulating anteriorly with the lacrimal bone and posteriorly with the orbitosphenoid. The lacrimal bone extends on to the facial aspect of the skull, and the lacrimal foramen is situated about 2 mm. in front of the orbital margin. A small ethmoidal foramen is present at the posterior extremity of the fronto-ethmoidal suture, and there is a vascular foramen on the orbital surface of the frontal under cover of the supraorbital margin. The optic foramen, approximately 1 mm. in diameter, can be identified on the right side; immediately behind it is the sphenoidal foramen.

On the dorsal aspect of the skull (Pl. 1, fig. 3), the coronal, interfrontal, interparietal and lambdoid sutures are quite distinct. Strong temporal ridges extend forwards from the nuchal crest. They are separated by a distance of not less than 10 mm., and at the level of the coronal suture they deviate laterally to the supraorbital process of the frontal bone. In their wide separation the temporal ridges resemble most of the Recent Lorisiformes, but contrast with *Galago crassicaudatus* in which the ridges are closely approximated in the adult skull and may fuse to form a median crest. The supraorbital processes of both sides form symmetrically pointed projections and thus at first sight give the impression that they may not have been continued into a postorbital bar to complete an orbital ring. However, as already noted, small surface abrasions of these processes on both sides, and of the supraorbital margins in front of them, make it impossible to be certain on this point. The temporo-parietal suture is distinct throughout its extent on both sides; in its contour it corresponds closely with that of *Galago crassicaudatus*. In the Eocene lemuroids *Adapis* and *Pronycticebus* there is a conspicuous opening for the sinus canal in close relation to this suture; in the present specimen, as in Recent Lorisiformes, it is absent.

The occipital region is marked by a sharp, projecting nuchal crest which extends transversely to continue with the suprameatal crest on the lateral aspect of the skull. Below it, the surface of the occipital bone extends down vertically to the upper margin of the foramen magnum. The surface contour of this part of the occipital region presents a primitive appearance which among Recent Lorisiformes is only approached by *Galago crassicaudatus*, but in the latter the nuchal crest is not so strongly developed. The plane of the foramen magnum is inclined at an angle of approximately 45° to the horizontal plane of the palate; its sagittal diameter is about 6 mm., and its transverse diameter 8 mm. The occipital condyles are closely similar in shape, extent and disposition to those of Recent Lorisiformes.

From the basal aspect of the skull (Pl. 1, fig. 4), the large size of the palate in relation to that of the base of the brain-case is a conspicuous feature. Its antero-posterior length is 27 mm., and its maximum width between the medial margins of the last molar teeth is 16 mm. The oval anterior palatine foramina are situated close to

the alveolar margin and measure 2·4 mm. by 1·4 mm. None of the palatal sutures can be accurately defined. In the mid-line the posterior margin of the palate forms a blunt point; the posterior margin of the nasal septum is continuous with a well-marked median ridge, which extends the whole length of the sphenoid and basi-occipital bones as far as the anterior margin of the foramen magnum. The suture between the pre-sphenoid and basi-sphenoid elements is distinct, but the latter is completely fused with the basi-occipital. Portions of the lateral and medial pterygoid plates are preserved, especially on the right side, and show no appreciable difference from those of Recent Lorisiformes.

The tympanic region of the skull shows several interesting features which differentiate it from any one of the modern lemuroid genera. There is no inflated bulla such as is found in all the Recent Galaginae, as well as in *Arctocebus* and *Perodicticus*. In this character the fossil skull differs from the modern African Lorisiformes and resembles *Nycticebus*. Laterally, the petrosal bone forms the free margin of the auditory aperture without being extended into a meatal canal; the margin is roughened and corrugated. The auditory aperture has a diameter of approximately 5 mm. On both sides the tympanic ring (ectotympanic) can be identified; on the right side it is seen to extend downwards slightly under cover of the free margin of the petrosal. The Lorisiformes contrast with the Lemuriformes by the fact that in the former the ectotympanic is placed superficially and, becoming somewhat expanded and applied to the outer margin of the petrosal, contributes to the formation of a narrow zone of the bulla wall at its lateral margin, whereas in the latter it remains a simple, free ring of bone enclosed within the bulla. At first sight, therefore, the appearance seen in the fossil skull suggests a slight approximation to the lemuriform condition. However, an examination of adult skulls of *Galago crassicaudatus* shows an appearance which is very similar except that the tympanic ring is not so clearly defined as a distinct element, and in most specimens can be seen quite clearly to expand ventrally to take part in the formation of the bulla wall. While the condition in the fossil skull is in strong contrast with the disposition of the free intra-bullar ring of the Lemuriformes, it thus appears to be rather more primitive than in the Recent Lorisiformes.

The mastoid region behind the auditory aperture forms a local convexity which is not so prominent or extensive as the inflated mastoid region of the modern African Lorisiformes. In this respect the fossil skull shows a closer approximation to the Asiatic genera. A small slit-like foramen lacerum is present at the junction of the petrosal with the alisphenoid. In the modern lorisiform genera this foramen is usually much more conspicuous, forming a relatively large, oval aperture. In the genus *Galago*, however, it may be smaller. The foramen ovale and the jugular foramen are both distinct and show no special features.

Dentition

The molar teeth are all preserved on both sides of the specimen, and also the last premolar of the right side. They are in good condition except for a slight degree of weathering of the enamel surface. The other premolar teeth, the canines and the incisors are represented only by their sockets or root stumps. As in modern lemurs

the dental formula of the upper dentition is 2 1 3 3. The main dimensions of the preserved teeth are:

	P^4	M^1	M^2	M^3
Antero-posterior length	2·8	3·5	3·8	3·5
Transverse breadth	3·0	4·2	4·8	4·3

The central incisors are very small, the sockets and exposed root stumps having a diameter of 0·8 mm. They are separated by an interval of 4·4 mm. The sockets of the lateral incisors have a diameter of 1·2 mm., and it is evident that these teeth were distinctly larger than the central incisors. In their relative size, therefore, they appear to differ from all Recent Lorisiformes, for in the latter the two lateral incisors are either approximately equal in size to the medial incisors, or the lateral incisors are much more reduced than the medial. Indeed, in some local varieties of *Nycticebus* the lateral incisor may be absent.

The root stumps and sockets of the canines show that these teeth were relatively large. The sockets measure approximately 3·0 mm. in antero-posterior diameter and 2·0 mm. transversely. They are separated from the anterior margin of the socket for P^2 by an interval of 1·4 mm. P^2 and P^3, so far as can be judged from the sockets and root stumps, must have been quite similar in relative size to those of *Galago crassicaudatus*. P^4 is a simple bicuspid tooth, the lateral cusp being the larger. There is a distinct internal cingulum, and also an external cingulum which forms anteriorly a small parastyle. All the premolars have two roots. It is to be noted that in its simple structure P^4 differs markedly from that of *Galago* in which the corresponding tooth shows a considerable degree of molarization, but it quite closely resembles P^4 in *Perodicticus* and *Nycticebus*.

The molar teeth all present a very well-defined tri-tubercular pattern, both the paracone and metacone being joined to the protocone by clear-cut and continuous enamel ridges, and the three cusps are of approximately equal size. In their simple construction they resemble those of *Perodicticus* and *Arctocebus* more closely than other Recent Lorisiformes. Except for the last molar, there is also a well-developed hypocone which is somewhat smaller than the protocone and separated from it by an intervening groove. On the medial and posterior aspects of the base of the cusp is a slightly developed internal cingulum. The hypocone is more strongly accentuated than it is in *Arctocebus* or *Perodicticus*, but approaches the latter more nearly. On the other hand it shows a marked contrast with *Galago*, in which the cusp is large and forms a lobular projection directed medially and backwards. In the Asiatic Lorisiformes the hypocone is relatively smaller and not so sharply defined. Perhaps the most distinctive feature of the upper molars is the conspicuous and thick external cingulum, which is elevated to the level of the occlusal surface of the crown. In this character they contrast with all the Recent Lorisiformes. In the latter an external cingulum appears to be present as a distinct and continuous ridge only in *Arctocebus*, but in this genus it is much finer and is confined to the base of the cusps. The last upper molar is reduced in size and the hypocone is absent, but there is a rather sharply defined cingulum at the posterior margin of the tooth. Except for the strongly developed external cingulum, the last molar resembles very closely in shape and relative size that of *Arctocebus*; in the other Recent Lorisiformes it has undergone a greater reduction in relation to the other molars.

DISCUSSION

The fossil lemuroid skull described above shows an interesting assemblage of morphological characters not found in combination in any of the Recent lorisiform genera. It resembles the modern African Lorisiformes, but the contour of the occipital region, the relatively large palate, the absence of an inflated bulla, the size of the nasal aperture, the small foramen lacerum, the less inflated mastoid region, the relatively large size of the lateral incisor and the presence of a strong external cingulum on the upper molars appear to be more primitive features. It differs from *Galago* in the simple construction of P^4 and the small size of the hypocone in the molars; in these two characters, as well as the absence of an inflated bulla, it approximates more closely to the Asiatic Lorisiformes. Except for the external cingulum, the pattern of the upper molar teeth is somewhat similar to those of *Perodicticus*, but it differs from this genus in the larger size of the last molar. The wide interval between the central incisors indicates the presence of procumbent incisors in the lower dentition. As previously reported (Le Gros Clark & Thomas, 1952), this condition is indicated, though not so extremely as in Recent Lorisiformes, in the fragmentary mandibular specimens which have been found on Rusinga Island. The skull differs markedly in its size and shape from the fragmentary skull from Rusinga Island previously described, and also in the construction of the tympanic region. It is certain, therefore, that the two specimens represent types which are at least specifically, and probably generically, distinct. The upper molars are also very different from those which have been described in the only maxillary fragment found on Rusinga Island in which they are present, for in the latter (R.106, 1948) the upper molars are much smaller, there is no external cingulum, and M^2 possesses only a very small cingulum hypocone.

The generic and specific identification of this new specimen must remain uncertain until more complete material from the Miocene beds of East Africa becomes available for comparative study. It may be conveniently allocated for the present to the genus *Progalago*, but its allocation to one of the species already defined on the basis of the lower dentition is not possible in the absence of the mandible. Although the fossil lemuroid material from East Africa is still very meagre, it is sufficient to demonstrate that in the degree of their speciation the Early Miocene Lorisiformes of Africa were probably as diversified as they are to-day.

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EXPLANATION OF PLATE

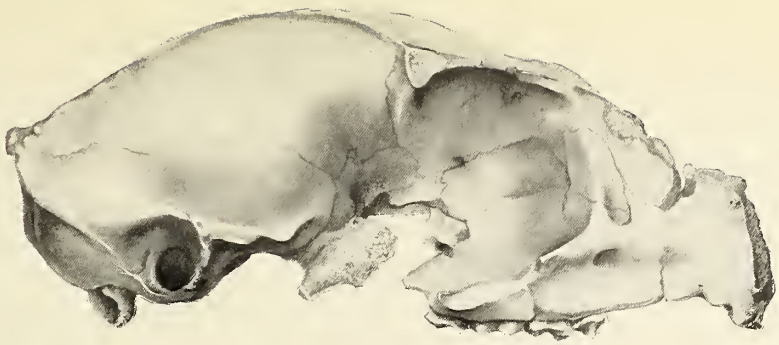
PLATE I

EXPLANATION OF PLATE

Progalago sp.

FIGS. 1, 2. Lateral views of the skull.
FIG. 3. Dorsal view.
FIG. 4. Basal view.

All figures × 2.



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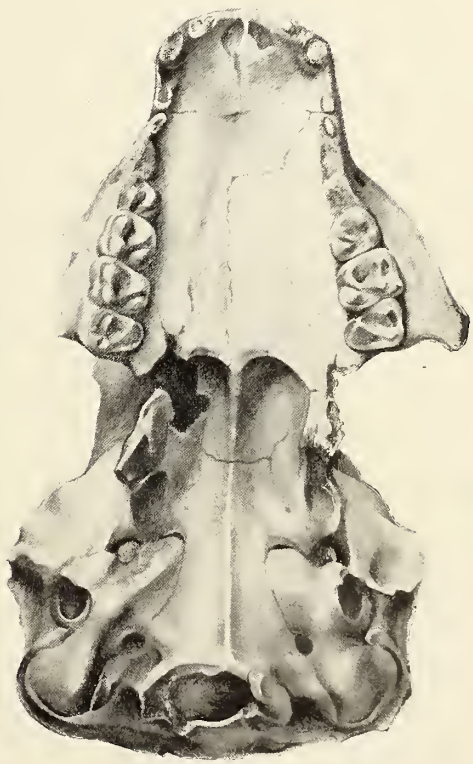

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PROGALAGO SP.